THE EDAPHIC FACTOR IN NARROW ENDEMISM. I. THE NATURE OF ENVIRONMENTAL INFLUENCES

Herbert L. Mason

There are three aspects to the dynamics of any problem involving the geographic distribution of plants. First there is the environment, represented by a series of intensity spans of the various environmental factors or by conditions or sequences of conditions of these factors. Secondly there are the physiological reactions of the individual plant that function within limits of tolerance for the conditions prevailing within the environment. Thirdly there are the genetic processes that operate to fix tolerance ranges of and give character to the individual, to control the variability of the population, and to give rise to new individuals preadapted to this environment or endowed with the potentiality for extending the area of the species. The interaction of these three forces determines the area occupied by any group of plants and no other force, except as it may influence either directly or indirectly the interaction of these three, can in any way affect the distributional pattern of the population.

The functioning of all plants is conditioned by environmental factors acting to control physiological processes. The relationship between environment and physiology in each individual case is probably genetically fixed as to the nature and span of the tolerances concerned. The fixation of tolerance spans may result from any of the isolating mechanisms of genetics that function to elaborate plants over the available habitats, each species or population being restricted to the area of the environmental conditions to which the tolerances of its component members are suited. These dynamics apply to all plants, hence all plants are restricted in range. Restriction in range is purely relative and is always related to environmental factors through physiological and genetic processes.

When the literature dealing with the subject of endemism is reviewed in the light of these ideas it becomes evident that there is much misunderstanding of the problems that relate to species of highly restricted range. Most of the difficulties result from an attempt to apply abstract ideas in the role of factors in cause-and-effect relationships. There are frequently encountered such terms as "age factor," meaning either age of species or age of land mass; "size factor," inferring size of land mass; "isolation," as a causal factor rather than as a term descriptive of a situation in which the real causes operate; and "historical factor," used in a vague sense to imply causal relationships bound often to unknown events of the past. I shall return later to a discussion of

Corrected date line: Madroño, Vol. 8, pp. 177–208. May 15, 1946.
Madroño, Vol. 8, pp. 209–240. August 5, 1946.

these abstractions. For the present it will be sufficient to point out that none of these concepts can be applied with significance to problems of physiological reactions of the individuals of the population or to the genetic processes that control a population. They can therefore have no influence in the restriction of area of any species of plant. The many difficult problems relating to endemism can never be solved by continuing to apply abstract ideas toward their solution. Endemic species, like every other species of plant, are made up of individuals that are functioning organisms. Their physiological reactions operate under the influence of environmental conditions. Their precise nature is the result of genetic processes. The general dynamics applying to problems of their geographic distribution must therefore be the same as those applying to all plants. Since there is so much misunderstanding of these problems, I deem it pertinent, before entering upon my subject, to discuss very briefly what I presume to be the nature of the roles of the environment, of the physiology of the individual of the population, and of population genetics, as they operate in vegetation dynamics. Although certain aspects of broad endemism are herein discussed, it should be borne in mind that the main thesis of this paper is the highly restricted patterns of distribution.

The Nature of Environmental Relations

The geographic area occupied by any group of plants is controlled by definite intensity spans or rhythmic patterns of certain conditions of environmental factors. Climatic factors in any given region are most inclusive in their scope of control. They may function within a pattern laid down by diurnal and seasonal rhythm. The nature and sequence of this rhythm may at times be a limiting factor to the occurrence of certain species of plants and may be equal in significance to the extremes (8, 10) of the intensity span of any environmental factor in its function of determining and controlling the periphery of the area that any species can occupy. Practically the entire range of normal climatic situations over the surface of the earth provides suitable habitats for plant populations, given an adequate edaphic setting.

In any given region the various aspects of the edaphic factor operate wholly within the conditions superimposed by climate. They may be relatively stable in their occurrence and span of intensity, or they may fluctuate as a direct result of some chance climatic sequence of events or with the rhythm of climatic events, or their fluctuation may be imposed by biotic factors or diastrophic processes. Here again, where the fluctuation is rhythmic, the rhythm may function as a limiting factor much as does the rhythm of climatic events. An example of such a rhythm is the seasonal fluctuation in the position of the water table, or the seasonal fluctuation of the soil-moisture content in certain arid regions, or the seasonal sequence of salinity or of hydrogen-ion concentration in certain soil solutions. Almost the whole enormous range of edaphic situations provides suitable habitats for some plant populations.

The biotic factor, being the result of the functioning of organisms, is in itself subject to the whole gamut of environmental factors, hence its various aspects operate within conditions prescribed by climatic and edaphic factors. Often the precise biotic effect may result from the regular coincidence of one phase of a life cycle with a certain phase of the life cycle of another organism upon which it depends or which it may influence. The yucca moth must emerge at the time that the yucca is flowering or no pollination will result. Here is a case of the necessity for the coincidence of two ontogenetic rhythms to insure proper functioning. Any factor that disturbs either of these rhythmic sequences to the extent that these two ontogenetic phases no longer coincide, would cause the yucca to lose its capacity to reproduce. There are many biotic environments that possess their special floras; frequently they consist of populations of single species and they often involve various aspects of parasitism and hemiparasitism.

It will thus be clear that the problems of environmental factors in their conditioning reactions on physiological processes of plants are not always simple problems of presence or absence, nor are they always simple problems of intensity or the gradient between extremes. They may involve the coincidence of many rhythmic sequences of fluctuating presence and absence, or fluctuating intensities with fluctuating physiological demands, or rhythmic sequences in the ontogeny of the plant. Often they operate to condition one another and may, in so doing, alter the physiological response. Most significant to problems of plant geography is the fact that environmental conditions occupy area independently of whether any precise condition may or may not influence a particular organism.

The Physiology of the Individual

The response of the organism to the conditions of its environment may be expressed in terms of the principle of limiting factors (8), and the theory of tolerance (7) or the theory of physiological limits (3); such relationships, insofar as they are inherent within the species, are subject to the laws of evolution and genetics. Within the species or population, the range of variation of the capacity to tolerate various aspects of the environmental factors is the direct result of the genetic diversity of the species or population in question (9). The functioning of all plants, regardless of their degree of geographic restriction or the age of the species, is conditioned by environmental factors acting or interacting to control physiological processes. Just as there are rhythmic aspects in many types of environmental factors, there are rhythmic aspects in the diurnal and seasonal phases of the plant's physiology as well as in the seasonal aspects of its ontogeny. Each phase of the rhythm of ontogeny or the rhythm of physiology is controlled by its own span or sequence of environmental conditions, and one phase of the ontogeny or physiology may make different demands upon the environment than another. Thus, some plants require a significant drop in temperature at night; others require a reasonably sustained temperature. Some plants come into flower under the influence of a seasonal sequence of rising temperatures and sustained water supply, while others, such as the summer annuals of the California foothills, appear to require a seasonal sequence of rising temperatures and decreasing water supply. During the occasional season when water supply is sustained, these plants spend most of their energy in developing foliage, and they produce few flowers, or flowering may be seriously retarded seasonally. Owing to the great mortality of seedlings between germination and establishment in nature, one must conclude either that some physiological process has a very narrow span of tolerance for some factor of the environment, or that the coincidence of a physiological or ontogenetic rhythm with some aspect of seasonal rhythm of the environmental complex is under very fine adjustment. An example is the environmental condition that controls the establishment of seedlings of the highly restricted endemic Monterey cypress, *Cupressus macrocarpa* Don, in its native habitat. In a normal year the moisture content of the surface soil recedes very rapidly at the end of the rainy season. If the growth of the taproot of the seedling is able to keep pace with the recession of the soil moisture the seedling will become established. If not, the seedling dries up and dies. Here an essential coincidence between two rhythmic cycles is usually out of adjustment and normally results in no establishment of seedlings. It is only occasionally that conditions are favorable for the establishment of seedlings of this species in its native habitat. Favorable conditions may result from late rain or a cool spring, and during such occasional years the establishment of seedlings is abundant. It is well to point out here that this is a problem of the relation of a species to its environment involving the species as it is constituted genetically and physiologically today, meeting environmental conditions as they prevail today. Given a plant so constituted and an environment so characterized, the age and source of the species to which it belongs, or the incidents in the history of the species, have no bearing on the problem of how the plant reacts to the conditions of its environment except as conditions and incidents of the past, reacting on the developing species population, may have influenced the genetic processes responsible for the present constitution of the plant.

The physiological processes of the plant, whether they involve nutrition, respiration, growth or reproduction, operate under the influence or sanction of environmental conditions. The environment functions to control the physiological processes, and, because the conditions of the environment occupy area, they circumscribe the area in which the process can function. Thus the dynamics of the physiology of the individuals of a population become linked with the dynamics of the environment to control the area the population can occupy.

The Role of the Genetics of the Individual and of the Population

Genetics, by whatever mechanism it may operate, in each individual case functions to set the capacity of the plant to tolerate the conditions of the environment. Once the zygote is formed, the role of genetics, so far as the new individual and its characteristics are concerned, is ended. This however is not the case with the population. The population is continuous beyond the life span of the individual. Its continuity results from the reproductive process among individuals which inevitably sets in motion the mechanics of population genetics. Each of these aspects of genetics plays an important role in the dynamics of plant geography.

There is enough evidence now at hand to justify the general conclusion that the relationship between function and its conditioning environmental factors is genetically fixed within each individual plant. The tolerance span of the individual is but an increment of the total span of variation that characterizes the species or the population with respect to any particular function and its conditioning environmental factors. Furthermore, the fixing of the tolerance span of the individual, or of the population or of the species, may result from any of the isolating mechanisms operating in the genetics of plants. Out of the diverse mass of seed presented to it, the environment is able to select only those individuals that are preadapted by their tolerance spans to become established and survive under the conditions prevailing in the area into which the seeds chance to fall. This repeated selection, generation after generation, tends to fix the form and the physiological capacity of the individuals of the species and to control the range of genetic diversity of the population that may occupy an area characterized by any given set of environmental conditions. It is akin to what Turesson (14) termed a "genotypical response of the plant species to its habitat." It results in a genetic race thoroughly in adjustment with the pattern of interaction between the various factors of the environment and the physiological processes of the plant that govern germination, establishment, and the functioning of the mature individual. It is through these processes that the species is enabled to persist in a given environment through the normal fluctuation of habitat conditions. It is likewise through these processes of genetic variation that individuals develop that are capable of extending the population into new habitats. Only in this way can a species overcome the great environmental diversity that otherwise would serve as a barrier to its migration. Many aspects of the edaphic environment do not migrate with climatic changes; these, therefore, stand as either selective agents or barriers imposed across the path of a migrating flora. Thus, extensive migration, even though it accompany a definite climatic environment in its shift, will probably result in considerable ecotypic differentiation and speciation, as well as in some extermination at various points in its course. To our thesis it is most important that the seed destined to survive in the new environment arrives already preadapted to the new conditions through the genetic phenomena that are inherent in the reproductive process. The new environment plays no part in this preadaptation.

Because of the nature of the usual reproductive process, every problem involving the geographic distribution of such plants must of necessity be concerned with the genetics of populations. The mechanics of population genetics have inherent in them the potentialities for inducing or restricting morphological and physiological variation in the population, as well as for initiating and pursuing the various processes leading to speciation that may function to elaborate the population over the available habitats. These mechanics owe their amplitude in any given environment to such things as the genetic diversity of the population, the nature and rate of mutations, gene infiltration, and the chromosomal phenomena that may alter the nature, arrangement, and quantity of genic materials entering the zygote, as well as to the selective influences of the conditions of the environment. Any of these phenomena may function to alter form and physiological responses of the individuals of the population and thus give rise to habitat types adapted to the particular environmental complex or complexes prevailing in the area. The population may operate wholly within its own genetic influence and become stabilized through random fixation, or it may be subject to frequent mutation or to gene infiltration that will function to keep it in a relatively unstable condition genetically. Whatever the situation may be, for purposes of plant geography it must be constantly borne in mind that the genetic phenomena involving the individual of the population, as well as the population as a whole, concern the physiological responses of individuals to the conditions of the environment and therefore have an important bearing on problems involved in the area the population can occupy.

Genetic diversity within the population may be expressed in terms of biotype number. At any given time biotype number in the population is the result of the interaction of genetic and physiological processes and environmental factors. This being the case, so far as the environmental relations are concerned, the number of biotypes in an area is to be determined by environmental conditions and not by the size of the area. Aside from purely environmental relations, the number of biotypes in an area is subject to such genetic phenomena as chromosome aberrations, gene infiltration, and random fixation. Thus, when conditions are alike over a wide area and genetic phenomena relatively stable, one might find few biotypes over the entire area. When great environmental diversity prevails in a small area and genetic instability characterizes the population, there may be many biotypes in a small area. On the other hand we may have, as Stebbins (13) has pointed out, a definite correlation between restriction of species and biotype depauperization. Here, in all probability, there must also be a close relation between environmental condition and adjusted tolerances resulting from biotype depauperization of the population. It must, however, be pointed out that the phenomena reported by Stebbins may not always of necessity be reflected in reduced size of area. It will be so only when tolerance spans are reduced along with biotype reduction, and the conditions to which the adjustment is suited occupy smaller area.

This discussion of the relation of the organism and the species population to its environment is pertinent to my subject because it demonstrates that the variations possible in the interaction of an enormously complex series of environmental factors with the physiological mechanisms of plants under the influence of ordinary genetic processes are sufficiently great to give rise to a plant population with all of the peculiarities of minor speciation and distribution pattern known to us today. It should be clear that the populations of special environments result from genetic differentiation. This is essentially the mechanism behind floristic diversity, a condition that obviously is to be associated with environmental and genetic diversity in their effect on physiological processes. The key to the problem is diversity. The greater the environmental diversity the broader the selective powers of the environment. It must follow that the greater the genetic diversity, the more numerous will be the opportunities for the exercise of environmental selection. The precise outline of the geographic occurrence of a species will be determined by the outlines of one or more increments of the pattern of environmental diversity. The nature of the species will result from genetic processes under the influence of environmental selection.

Endemism, Area and Geographic Restriction

For these reasons all plants are restricted in their geographic area by environmental conditions, and, for these same reasons, all plants are, in a sense, endemics. The area of their occurrences is determined by precisely the same set of dynamics. It would appear that endemism results from forces operating to limit or restrict the area of all species, and that the nature of these forces is the interplay or interaction of environmental factors on physiological and genetic processes. The manifestation of restriction may be in the form of a response to climatic, edaphic, or biotic factors, or to any combination of these. There is evidence that all of these, singly or in various combinations, have been responsible for some aspect of endemism. Endemism should not be burdened with indefinable presumed freak distribution patterns, nor should it be confined to highly restricted patterns of distribution. When so treated it is set upon a plane where normal explanations seem not to apply. It should be constantly borne in mind that the dynamics of plant distribution are essentially the same or of the same order for all plants, and that these dynamics may serve as a pattern or framework upon which to build interpretations or explanations of the many problems of either usual or unusual distribution.

With this concept of endemism we have in no way altered the problem; we have altered only the point of view. We still have restricted endemism and broad endemism, old species and young species, and all stages in between. We still must seek explanations in terms of cause and effect. With this point of view, however, *area becomes subordinated to environmental condition. The area is incidental to the condition and is significant only because the condition occupies area.* Environmental diversity becomes the key to floristic diversity, and the more precise patterns of distribution must be involved with the more precise causes. In general, the larger the area occupied by a species the more apt is its periphery to be under the influence of a complex series of limiting factors. These may operate differently in the various segments of the periphery of the area of the species. The smaller the area occupied by the species the fewer will be the factors concerned with its restriction until, in certain highly restricted patterns of distribution, a single limiting factor may suffice. Although this relationship is in general true, it obviously cannot be absolute because it is perfectly possible for a single factor or a few factors to control fairly large areas or for small areas to be controlled by several series of factors.

The causes behind any particular pattern of geographic distribution of plants may be numerous and diverse. They must, however, be of the nature of conditioning factors to physiological processes. Since their chief manifestation is a pattern of geographic distribution within an area, it follows that the causes must be related to conditions that likewise occupy area independently of the fact that plant species may be restricted by them. Of the three aspects of the dynamics of plant geography, only that pertaining to the environment independently occupies area. Therefore we may conclude that causes behind any patterns of distribution are intimately linked with the environment, and that the distributional patterns are circumscribed by environmental conditions. It is the areal span of the environmental condition to which the plant is preadapted that determines the area that any species can occupy. If the condition is local, the potential area of the species will be local; if the condition is widespread, the potential area of the species will be broad. Likewise, if the area of the condition is continuous, the potential area of the species is continuous; if the condition is discontinuous, the potential area will be discontinuous. This does not mean that all plants occupy all of their potential area, but it does mean that all plants have a potential area characterized by a given set of environmental conditions occurring in a definite span of intensity and often in definite rhythmic sequences. The plant, having the capacity to tolerate a particular set of environmental conditions, will—unless effectual barriers exist—soon occupy all of its potential area through such agencies of regular and chance dispersal as may be available to it.

When we begin with the concept that all species owe their distributional patterns to various aspects of the same set of dynamics, we note that there are wide variations in the size and nature of the area occupied by the different members of the flora. We observe that there appear to be patterns of distribution that relate themselves to various sets of environmental conditions. Some species will appear to be under the influence of certain aspects of climate, such as temperature or moisture. Other species may seem to be under the influence of edaphic factors, such as the physical conditions of texture or of water-yielding capacity of soil or perhaps some local occurrence of a special metallic ion in the soil solution. In other cases some aspect of a biotic relationship may prevail. Were it possible to make a really adequate analysis of such problems we probably would find that almost every conceivable combination of environmental condition could be correlated with the distributional pattern of some species of plant. It must be emphasized that any environmental factor or combination of factors may be responsible for the restriction of area of some species of plant. In all probability the environmental relations of the distributional pattern in any given case involve complex interrelationships of several aspects of one or more categories of factors. Nevertheless, it is also highly probable that in other cases a single aspect of the environment may occur spatially in such a manner as to precisely circumscribe the periphery of the area, or a segment of the periphery of the area, that the species can occupy. Presumably this condition of the environment at this point spatially represents the limit of tolerance for a vital function, or marks the point where two or more coincident rhythmic cycles cease to be coincidental. It must be emphasized that the entire periphery of the area occupied by a species is not necessarily under the control of the same factor. An example may be cited in the case of the distributional pattern of *Sequoia sempervirens* (Lindl.) Dec. Its northward extension appears to be limited by low winter temperatures, particularly as these affect seedlings; its eastern boundary coincides with the boundary of the occurrence of almost daily summer fog; to the south some other aspect of water relations of soil or atmosphere, or possibly the oxygen content of the soil solution may be the limiting factor; to the west it is against the barrier of the Pacific Ocean; a thirty-mile gap in its range coincides with the occurrence of an extensive area of serpentine rock. At many points along its front any number of minor factors may control the situation locally. These are different categories of environmental factors, and for the most part they are critical at different seasons of the year. In the case of highly restricted patterns of distribution, however, it is more probable that the entire periphery may be, in most cases, under the control of a single environmental factor or a single complex of factors. This is especially true where the limiting factor may be edaphic.

The Edaphic Factor

When we consider the nature of environmental factors whose various conditions may occupy area independently of the occurrence of any species of plant, it seems probable, except for certain cases of special biotic restriction, that the edaphic factor occurs spatially in a manner that is most apt to be related to highly restricted patterns of distribution among plants. The edaphic factor pertains to the substratum in which plants grow and from which they derive their mineral nutrition and much of their water supply. It involves the physical and chemical nature of the substratum together with the effects of these on the various aspects of water relations and aeration of soils. Because of the great local variation that exists in the physical and chemical nature of the substratum and soils, the edaphic factor presents the possibility of enormous diversity of habitats in any given area. This diversity is expressive of conditions that may involve presence or absence, amount, degree of intensity, or rhythmic sequences of fluctuation of any aspect of the edaphic factor as it may vary from place to place and from season to season in the area. Because of the nature of various conditions of the edaphic factor, the geographic area of the condition is often very sharply delimited.

Edaphic diversity owes its nature to many causes and may express itself both physically and chemically. Without attempting to give a complete picture of the causes of this diversity, the nature of some of it may help to clarify certain aspects of the problems of highly restricted plants. Most obvious in the cause of edaphic diversity is variation in the position of the water table. Where it occurs above the ground level we have lakes, ponds, pools, and marshes. Its depth below the ground is no less significant as an ecological factor. The seasonal fluctuation in the position of the water table presents a rhythmic sequence that is very important floristically, especially in arid and semi-arid regions. Where these conditions coincide with particular soil types, special habitats of a highly selective nature are produced. Among these are the vernal pools of the Great Valley of California with their richly endemic floras.

Soils, soil building, and soil leaching provide other aspects of edaphic diversity; here are many forces at work that may produce very local conditions. Soil building and soil maturing, by bringing together and mixing many diverse sediments, tend in some cases to counteract some of the elements of diversity characteristic of certain of the more youthful, highly mineralized situations. Hence, greater floristic diversity sometimes occurs where soils are less mature. Of possible significance to our subject is the ability of certain plants to absorb certain rare earth minerals from the soil and concentrate them in the leaves. When these fall and decay the minerals are deposited in the surface layers of soil in unusual concentrations. It is now an established fact that yttrium is accumulated in unusual quantities in the surface layers of the soil by the disintegration of hickory and walnut leaves (11). Oak leaves from these same localities show no trace of yttrium.

Other causal factors of edaphic diversity are the forces responsible for both epeirogenic and orogenic diastrophism of the earth's crust. Here, through faulting and folding and subsequent wearing down and dissection of the uplifted segments, the various strata of rock become exposed, each with its own physical and chemical features and each producing its own effect on soils. The area and continuity of these outcrops will vary with the thickness of the strata, the length of the exposure, the degree of dissection, and the location of any overburden of soils or soil materials. In highly tilted or highly folded strata the area of some of the outcrops may be exceedingly small. Often all that may remain of a given stratum persists as a cap on the top of a mountain. The contact between strata often is a line of weakness through which water may seep and bring to the surface dissolved minerals, which it deposits in increasing concentration in the surface soils. Faulting and folding often disturb drainage conditions and the movement of water, altering the pattern of erosion and affecting problems of the water table.

The extent of edaphic diversity attendant upon the forces of vulcanism and other igneous agencies is enormous. On the slopes of a single volcano very diverse conditions may result from the nature of the activity and the chemical composition of the magma that wells up. Pyroclastics of various types may be thrown out and roughly sorted into different patterns over the surface, and these may become interbedded or intruded with lavas of various types. The speed of cooling will materially affect the nature of the resultant rock. Lavas filling fissures and forming dykes frequently cause contact metamorphism of the older rock. Superheated waters, often from great depths, come to the surface charged with compounds of metals or other minerals in solution, which they deposit at the surface. Fumeroles and other solfateric activity persist long after other activity ceases, adding new supplies of mineral substances to the surface layers. Molten lava often is a poor medium for rapid diffusion, and sometimes high concentrations of certain minerals remain local in the hardened lava, often in water-soluble form, resulting in a very diverse pattern of mineral concentration over the surface layer of such a lava flow. Of particular significance to our subject is the role of vulcanism and its attendant phenomena in bringing to the surface many minerals of types both useful and toxic to plants.

Still another cause of great edaphic diversity are the forces attendant upon geological metamorphism. Here significant physical and chemical change is wrought upon rock sometimes on a very wide scale and sometimes quite locally. Where these processes involve substitution, crystallization, and segregation of minerals, the infiltration of waters charged with minerals, and other attendant chemical changes under the influence of heat and pressure, situations are created that may result in very local geographic patterns of edaphic conditions when these rocks become exposed at the surface. Much of the concentration of metals in the earth's crust results from the forces of metamorphism. A great variety of rock type is the result of metamorphism, and it is significant that endemic species of plants are often associated with metamorphics. Outstanding among these rocks are the gneisses, schists, diorites, and serpentines.

Throughout this discussion of the edaphic factor there has been frequent reference to the concentration of minerals and metals in the surface layers of the earth's crust. This aspect of the environment will stand out as very important to anyone studying the problems of restricted distributions of plants, but, unfortunately, there is as yet very little information of a precise nature to enable the subject to be put into clear terms of cause and effect. From the nature of the areas where great concentrations of highly restricted species occur, it appears almost certain that some soil chemicals possess an inordinately high selective value on vegetation. One must not rule out the possibility that they might, in some instances, affect mutation and mutation rate or induce other chromosomal disturbances. Large numbers of restricted species occur on ultrabasic igneous rock and on metamorphics containing metals of the ferro-magnesian complex including in the soil solution (in concentrations often lethal to crop plants) such metals as the ferric irons, magnesium, manganese, chromium, nickel, cobalt, mercury, and most of the other basic heavy metals. Highly restricted endemism on serpentines and serpentinized rock almost the world over provides excellent examples. Here are variable high concentrations of iron and magnesium and, in some areas, local concentrations of chromium, manganese, nickel, cobalt, and mercury. In some of these areas the sparsity of the flora suggests high toxicity for most of the species readily available to them. The taxonomic peculiarity of the species that do tolerate these conditions suggests that these species, through genetic processes, have been preadapted to these conditions and, hence, that the seed from whence they sprang reached a habitat favorable for them to become successfully established. Gordon and Lipman (4) maintain that the peculiarities of serpentine soils are not due to toxic effects of magnesium, but rather to the unavailability of necessary mineral ions, to high hydrogen-ion concentrations, and to low concentrations of potassium, nitrogen, and phosphorus. Robinson, Edgington, and Byers (12) point to the high toxicity of such substances as chromium, nickel and cobalt, elements which are frequently found in serpentine soils in high concentrations, and attribute to these substances the usual sterility of serpentine soils. Certainly either of these ideas could well account for absence on serpentine soils, but to our subject it is more important that we account for the presence of species that tolerate these substances in such high concentrations. It is these species that make up the endemic element of the floras of such areas.

Foster and San Pedro (2) speculate on the rarity and lack of establishment of seedlings of *Microcycas calocoma* A. DC. in Cuba. It might be relevant to this problem to mention that *Microcycas* occurs in a region where some of the soils derived from chlorite contain the highest concentrations of chromium known in soils (12). Concentrations of from 3.18 to 5.23 per cent of chromic oxide occur locally. This substance is toxic to most plants in concentrations of about 0.1 per cent. Obviously, such soils would be highly sterile to most crop plants and such plants as do occur there can do so only by genetic adjustment of tolerances. Other minerals that seem related to problems of endemism are gypsum (6), diorite, quartzite, and some forms of calcium carbonate. In some instances the effect may be the result of associated minerals or metals not evident to the field observer.

It appears almost certain that some relationship exists between the highly mineralized nature of the substratum and the peculiarities possessed by the floras in such areas, but as yet we are not in a position to state just what that relationship might be. It is a subject that, through newly developed techniques, lends itself to experimental investigation; it is to be hoped that within the near future enough studies of this will be undertaken so that the problem at least can be narrowed down if not solved.

From the standpoint of highly restricted distributional patterns in plants it is important that of all of the environmental influences, the edaphic factor most frequently occurs in sharply defined patterns and often occupies very small areas. It is also important that the toxic substances possessed by certain soils or soil materials may, through restriction or special selection, produce striking vegetational results.

The Misuse of Abstractions

To round out this discussion of the environmental relations of endemism it is desirable to review certain features of previously suggested explanations of the problems of endemism that, to the writer, appear to be based upon fallacious reasoning. Since the time of Engler (1), it has been customary to regard endemics as being of two kinds: first, new species that have not as yet achieved their potential area, and second, relict species that are reduced from a former widespread area. These are two aspects of a single problem, age. Even though a species does possess age as one of its attributes, and even though its distributional pattern does fluctuate through time, no species ever owed its distributional pattern for very long to its age. Old species may be widespread or they may be restricted, they may be abundant or they may be rare. The same may be said of new species after the very brief interval necessary for them to achieve or occupy that portion of their potential area not denied to them by the existence of barriers. In general, each species will occupy locally the same size and configuration of area as do the conditions of the environment to which it is adapted. Age has nothing to do with this. To be sure, the processes that elaborate a species over the available habitats require time, and the longer the species has been in the area the more opportunities it will have had to become genetically elaborated, but it does not necessarily follow that this will happen. Likewise, environmental fluctuation that may serve to restrict or to reduce genetic diversity will vary in rapidity in different areas and in its effect on different species. These processes of distribution and change all require time, but time is not their cause. They may be rapid with one species or infinitely slow or non-existent with others. They may be rapid under one set of conditions and slow under others. These would appear to be individual problems under individual conditions. There is little in this situation to permit generalization as to age, time involved in expanding or receding area, or speed of evolution. Hence, both restricted and widespread species may well be of any age. Age is, therefore, not necessarily a significant attribute of any restricted endemic. Age is sometimes expressible in terms of biotype depauperization, but this need not necessarily imply that the area will be highly restricted or even small. The area that any species of plants may occupy stands as a fact apart from details of its age, so far as cause and effect are concerned.

The phrase "historical factor" is often applied to problems of restricted distribution. This is a vague way of implying that age is a significant factor or attribute of endemism, as well as being a phrase with which one may confuse facts attendant upon migration and establishment with facts pertaining to restriction of range. There is no doubt that species are characterized by age and that they have had a history. The history of a plant species may tell the very important story of *how* it arrived in any given place and *where* it came from, but it does not explain its persistence nor the precise pattern of the area occupied in the new environment. The facts pertaining to the pattern of area are tied up with the individual plants as they are constituted today and with the environmental conditions as they prevail today. Such facts are no doubt related to the past, but the past is not the key to them because it does not necessarily serve to explain them; nor are they necessarily the key to the past since they are the result of today's conditions. The term "historical factor" is thus another abstraction which too often is used without any clear notion of what it does imply.

Isolation is often referred to as a cause or contributing factor in endemism. Isolation may explain abstractly the conditions which operate to preserve or encourage genetic purity by preventing gene infiltration. It may also aid in maintaining reduced competition. But since neither isolation nor the condition that it implies plays a part in bringing the plant into existence or in preadapting it to the habitat, it cannot of itself initiate any endemic. In all of these supposed functions isolation is important for what it implies and not for what it of itself does. The plant comes into any given habitat as a seed already endowed by genetic processes with a tolerance range for environmental factors that determines its capacity to function. Isolation in any given habitat is merely a way of stating that the plant or the species has a sort of priority to function unmolested by forces that do not exist in this particular habitat. A factor that does not exist in a habitat never exercises any influence on the plants of that habitat. Isolation is an abstraction definable only in terms of negative forces. Neither it nor the absent factors that it implies can be a stimulus of utility to the functioning of any physiological or genetic mechanism. At this point the "Sewell Wright effect" (16) may be adduced to refute my contentions. However, in explaining the "Sewell Wright effect," isolation is a convenient mode of expression for what it implies. The significant point in the "Sewell Wright effect" is the existence of a small population operating wholly within its own genetic influence.

Because the above difficulties are involved in the concept of isolation, it becomes very important that facts be kept in their proper place. This may appear to be trivial quibbling over definition and concept, but by being precise here we are in a better position to understand why there is no striking endemism in many hundreds of isolated islands. In spite of their isolation, coral islands are notoriously lacking in specific plant endemism. Being essentially alike environmentally, these islands offer little opportunity for environmental selection to operate. Were isolation a causal factor in highly restricted patterns of distribution, there would be no reason why every island should not develop populations of highly restricted species.

Attempts have often been made to correlate the number of endemics in an area with both the size and the age of the area. As for size of area, it is to be expected that there will be correlation in numbers only when there is also relative habitat diversity. Age of area is an abstract expression which implies a complex series of problems involving such features as maturity of terrain, leaching of soils, and time required in genetic processes, all of which may conceivably have some bearing on the problem. But their effect could be completely nullified by lack of environmental diversity. Old land masses are not consistently inhabited by many endemics, and some newly available areas have several. On the other hand, it is conceivable that the factors implied by age of land mass, together with great environmental diversity, might produce numbers of endemics wholly out of proportion to either of these influences alone.

A great deal has been written about area and its significance in the interpretation of the development of vegetation and as a basis for the explanation of various historical trends. Since the plant is adapted through genetic processes to a given set of environmental conditions, the area the plant occupies is purely incidental to the condition to which it is adapted. It occupies this area only because these conditions prevail there. The size and the shape of the area occupied are the product of today's facts, both genetic and environmental. Area as such has no historical significance in vegetation. Thus the concept of "age and area" (15) loses its significance unless it can be established that the condition was expanding its area at a consistent rate or that the mutation rate, or the rate of other genetic phenomena that might enlarge tolerances, was uniform and persistent and was regularly producing types that could persist and expand the area of the species. Likewise, Hultén's idea of equiformal progressive areas (5) does not take these facts into consideration. Since size and shape of the area occupied reflect the occurrence of conditions, any correlation of area with history or historical sequences is strictly coincidental. The important point is that one would of necessity have to establish his historical facts independently of the pattern of distribution of species. The pattern of distribution is determined by causes inherent in the locality and most probably has had no correlative relationship with the history of the flora over any wide area. The type of plant occupying the area (the ecotype) in most instances must have been produced reasonably close to the condition under which it grows. Any species capable of extensive migration must, by the very nature of things, be exceedingly plastic, that is, it must be very diverse genetically and capable of meeting differing habitats with new ecotypes.

Documentation of some of the ideas herein expressed will follow as Part 2 of this paper in a subsequent number of this journal, wherein the nature and occurrence of concentrations of highly restricted species will be discussed.

Summary of Part 1

1. The dynamics of the geographic distribution of any species involves the interaction between the environment, the physiological processes of the individuals of a population, and the genetic processes that fix tolerances and maintain or elaborate the population and preadapt individuals to environmental fluctuations.

2. Endemic species differ in no significant way from (so-called) "ordinary" species in their dynamics; restriction in geographic range as it applies to endemic species is, therefore, of the same order—so far as cause and effect are concerned—as is the restriction of any and all other species.

3. The area occupied by any species is determined by factors whose various conditions occupy area independently of the fact that species might be restricted by them. Since only environmental conditions independently occupy area, it is the environment that determines the pattern of distribution of all plant species by permitting the functioning of only those individuals whose tolerances have been preadapted to the special conditions of the environment.

4. Of the various categories of environmental factors, the condition of any factor or combination of factors may serve to restrict the range of some species of plants. Of these factors, however, the edaphic factor is most apt to occur in sharply defined patterns and often in small areas. In this connection, the regular occurrence, the world over, of highly restricted species in association with the occurrence of certain minerals and metals in the soil solution, suggests that these substances play an important role in problems of geographic distribution of highly restricted species.

Department of Botany,
University of California, Berkeley.

Literature Cited

1. Engler, A. Versuch einer Entwicklungsgeschichte der Pflanzenwelt. 2: 48. 1882.
2. Foster, A. S., and M. R. San Pedro. Field studies on Microcycas calocoma. Memorias de la Sociedad Cubana de Historia Natural Felipe Poey 16: 105–121. 1942.
3. Goode, R. D'O. A theory of plant geography. New Phyt. 30: 149–171. 1931.
4. Gordon, A., and C. B. Lipman. Why are serpentine and other magnesian soils infertile? Soil Sci. 22: 291–302. 1930.
5. Hultén, E. Outline of the history of arctic and boreal biota during the

Quaternary period. Their evolution during and after the glacial period as indicated by the equiformal progressive areas of present plant species. Stockholm. 1937.
6. Johnston, I. M. Gypsophily among Mexican desert plants. Jour. Arnold Arb. 22: 145–170. 1941.
7. Livingston, B. E., and F. Shreve. The distribution of vegetation in the United States as related to climatic conditions. Carnegie Inst. Wash. Publ. no. 284: 1–585. 1921.
8. Mason, H. L. The principles of geographic distribution as applied to floral analysis. Madroño 3: 181–190. 1936.
9. ————. Distributional history and fossil record of Ceanothus. Van Rensselaer, M. and H. E. McMinn. Ceanothus. Santa Barbara. 1942.
10. ————. Review of Cain, Foundations of plant geography. Torreya 45: 17–21. 1945.
11. Milton, C. K., K. J. Murata and M. M. Knechtel. Weinschenkite, Yttrium phosphate dihydrate, from Virginia. Am. Mineralogist 29: 92–107. 1944.
12. Robinson, W. O., G. Edgington and H. G. Byers. Chemical studies of infertile soils derived from rocks high in magnesium and generally high in chromium and nickel. U. S. D. A. Tech. Bull. No. 471. 1935.
13. Stebbins, G. L. The genetic approach to problems of rare and endemic species. Madroño 6: 241–258. 1942.
14. Turesson, G. The genotypical response of the plant species to its habitat. Hereditas 3: 211–350. 1922.
15. Willis, J. C. Age and area. Cambridge. 1922.
16. Wright, S. Evolution in Mendelian populations. Genetics 16: 97–159. 1931.

A "NEW" CULTIVATED SUNFLOWER FROM MEXICO

Charles B. Heiser, Jr.

The study of the origin of the cultivated sunflower (*Helianthus annuus* L.) is still a relatively unexplored field. *Helianthus annuus* (including *H. lenticularis* Dougl.) is a complex assemblage of weeds of roadsides and city dumps, and of plants cultivated for their seeds or for ornamental purposes. From what is known at present it is assumed that the cultivated sunflower arose from a wild or weed type *H. annuus*.

The sunflower was introduced into Europe in the sixteenth century. In the 1758 edition of Dodonaeus (2) the sunflower is mentioned. The seeds of this plant are stated to be flat and long, and somewhat "browne" or "swarte," and formerly were grown in Spain. Gerard (3) in 1597 describes a sunflower with seeds "black and large," and goes on to describe a second kind of sunflower with the seeds "long and black with certain lines or strakes of white running amongst the same." It is quite probable that the sunflower was first introduced into Europe by the Spanish and that this was a black-seeded variety which in all probability came from Mexico or the southwestern United States. The introduction of the striped variety probably occurred at a later date and this plant may have been introduced from the northern United